THE RAY SYSTEM OF QUERCUS ALBA

LADEMA M. LANGDON

(WITH TWENTY-TWO FIGURES)

Introduction

The medullary rays of *Quercus alba* are of three distinct types: uniseriate rays, thin, linear sheets of tissue of a single layer of cells; multiseriate rays, two or more cells in width and many cells in height; and compound rays, which are broader than either of the first two mentioned and consist of extensive homogeneous masses of parenchyma. Between the uniseriate and the compound types there exist numerous transitional stages, representing either disintegration of the broad ray into a number of narrow ones or the integration of many uniseriate rays to form the compound rays. Figs. 9 and 10 illustrate these three principal types.

The evolution of these different types of rays and the relationships between them have recently been the cause of much discussion and the subject of a series of investigations carried on chiefly in the laboratories of Harvard University. This particular line of investigation was initiated in 1909 by JEFFREY (7) when he proposed the "aggregate ray hypothesis." He maintains that paleobotanical evidence points to the probable derivation of the existing oaks from ancestors which possessed only the linear type of ray, and that the broad rays so characteristic of the present oak wood have been formed by a gradual aggregation of uniseriate rays. His arguments favoring the "aggregate ray hypothesis" have since been perfected and worked out in greater detail by EAMES (5, 6) and by BAILEY (1, 2, 3). EAMES (5) has demonstrated from a study of fossil and seedling oaks that the broad type of ray has originated by the aggregation or fusion of many of the small uniseriate rays through the transformation of the included fibers and wood parenchyma into ray parenchyma. He agrees with JEFFREY (7) that in the fossil oaks and in the seedlings of modern oaks only the linear type of ray is found. BAILEY (2) has developed this particular theory and asserts that the great factor at work in the formation of the compound ray is the influence of the leaf trace. Since the stem adjacent to the leaf trace is the most natural storage place for food manufactured in the leaf, he concludes that the storage organs, the rays, would be enormously developed at this particular point in the stem for the purpose of storing assimilates descending from the large persistent leaves of Mesozoic angiosperms. Following its formation at the leaf trace, the broad ray has spread throughout the tree. These "foliar" rays, as BAILEY calls them, have persisted in the families of the dicotyledons either in their very primitive "aggregate" condition (composed of congeries of small rays) or in their more advanced "compound" condition (completely parenchymatous).

A second line of evidence which amplifies this original hypothesis is advanced by THOMPSON (8). He maintains that the "multiseriate" type of ray has originated from the diffused portions of "aggregate" or "compound" rays. With the advent of a severe winter season and the consequent acquirement of the deciduous habit by the leaves, the organization of storage systems about the leaf trace was no longer of advantage. Thus in the development of the multiseriate ray, which characterizes the majority of living dicotyledons, portions of the aggregate or compound rays have been diffused more or less uniformly throughout the stem.

In opposition to the aggregate ray hypothesis, BAILEY and SINNOTT (4) in a more recent article suggest the possibility that the clusters of small rays may be, in many cases, stages in the breaking down rather than the building up of wide rays. They state that the multiseriate ray has originated merely by the gradual increase in width of the primitive uniseriate ray, and that in all probability the so-called "aggregate" rays, instead of being formed by the fusion of many smaller linear rays, are merely stages in the reduction and disintegration of the wide multiseriate rays.

Material and methods

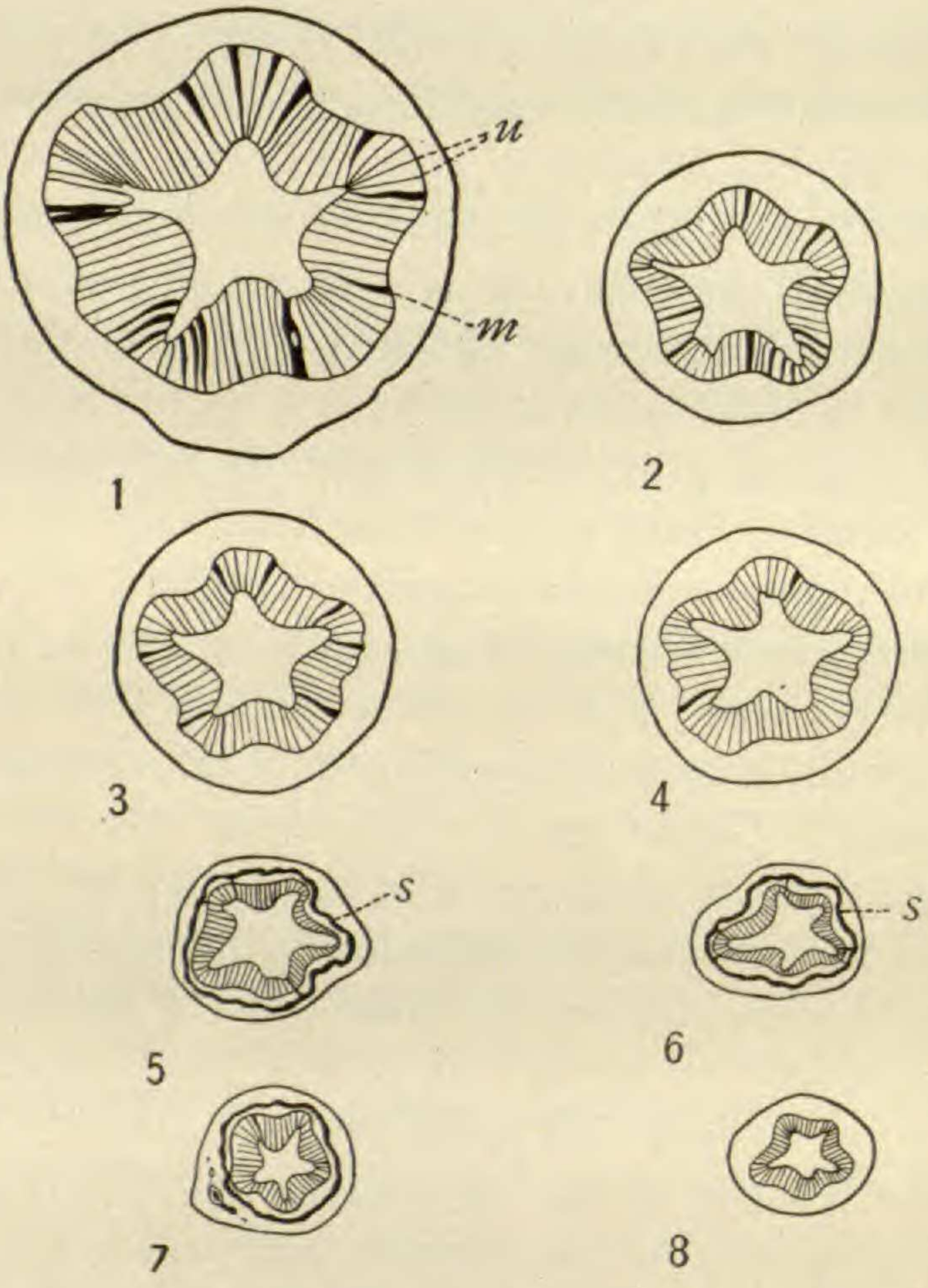
About January 1, 1916, specimens of white oak twigs varying in age from 1 to 19 years were collected from three different trees on the campus of Oberlin College and from three different regions of each of these trees. Likewise, from each tree twigs of unusual vigor of growth and shoots suppressed in their growth were procured. For convenience the trees were numbered I, II, and III. Trees I and III are of about the same age, 55–60 years old, but tree I is larger and of slightly more vigorous growth than III. Tree II is younger than either I or III, about 35–40 years old.

In the preparation of the wood for sectioning the process taken from CHAMBERLAIN'S *Methods in Plant Histology* was followed with slight modifications. The specimens of wood gathered from the different regions of these three trees were cut into small blocks and treated with hydrofluoric acid. After treating with the acid, wood should be left in equal parts glycerine and 30 per cent alcohol for several days or even weeks before sectioning to prevent the cortex of the stem from separating from the xylem.

A series of transverse and tangential sections, both nodal and internodal, was made of twigs of all ages from 1 to 19 years, taken from the lower, center, and top portions of all three trees. This afforded an opportunity to compare woods of the same age and vigor of growth from different parts of the same tree and also from different trees, thus to ascertain whether certain ecological conditions, such as age of trees and vigorous or suppressed conditions of growth, may not tend toward the modification of the ray system of *Quercus*.

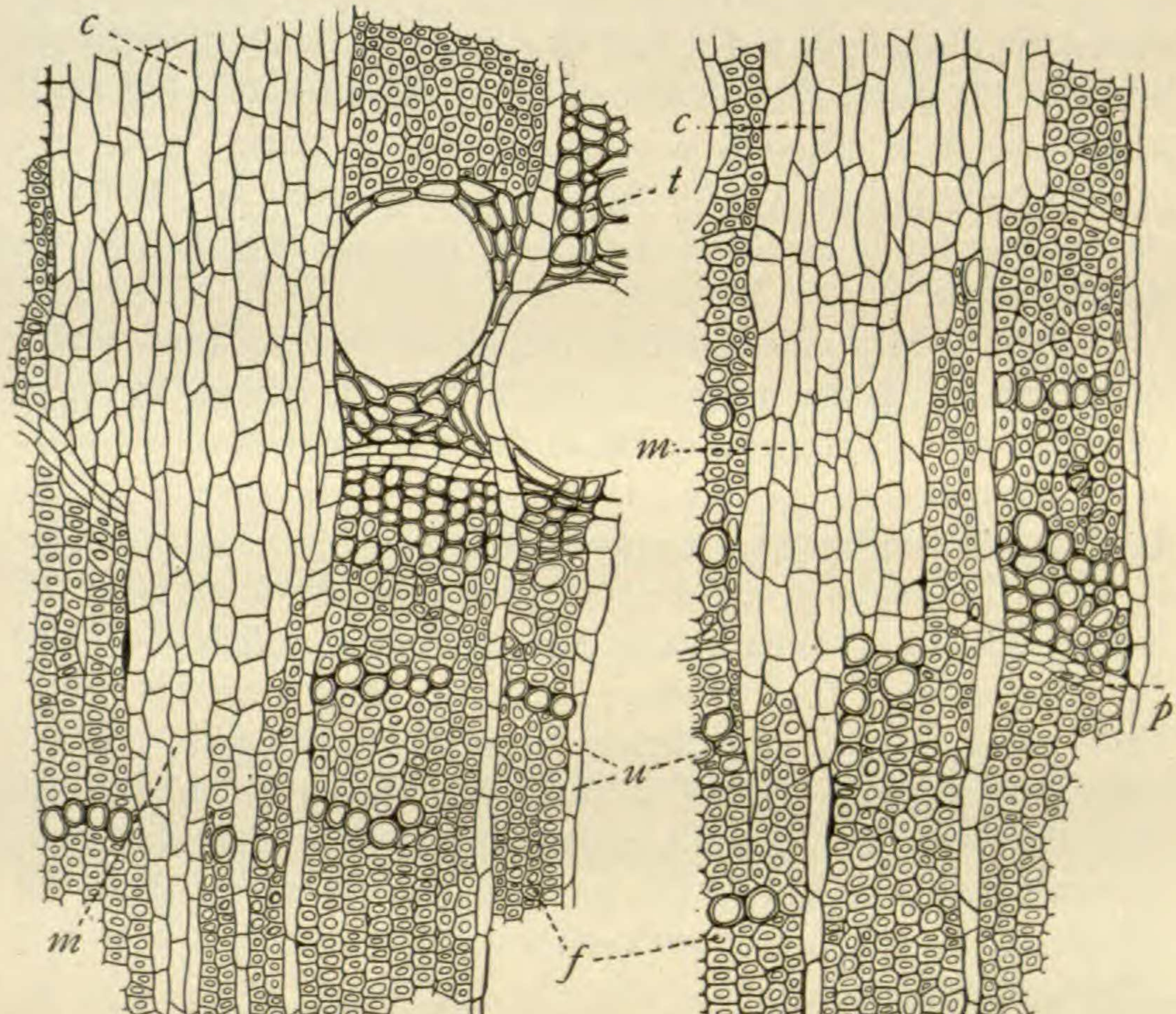
Observations

THE FIRST ANNUAL RING.—Although the uniseriate ray is the predominating type in the first formed secondary xylem of *Quercus alba*, multiseriate rays 2–6 cells in width also occur, radiating in pairs from the 5 lobes of the pith (fig. 1). Since these lobes or deep extensions of the pith into the surrounding woody tissue mark the region of leaf gaps, the initiation of pairs of wide rays at these particular points clearly indicates the relation of these rays to the two lateral leaf traces passing out at alternating nodes. Both the wide and the linear rays extend radially from the pith through the phloem to the band of sclerenchyma separating the phloem and cortex regions of the stem. The effect of vigorous growth upon the general structure of the stem, and especially upon the ray system, is particularly noticeable in the first annual ring. Not only are the multiseriate rays more numerous and parenchymatous, but the ring of growth is wider and the vessels and tracheids correspondingly larger in the vigorous (figs. 1, 2, 3, 4) than in the non-vigorous or suppressed year old twigs (figs. 7, 8).



FIGS. 1–8.—Transverse sections of year old twigs: fig. 1, section cut just above node, of unusually vigorous year old shoot from upper part of tree I; *u*, uniseriate rays, *m*, multiserate rays; figs. 2–4, sections cut just below node, from lower (2), center (4), and top (3) regions of tree I; figs. 5, 6, sections cut slightly below node of twigs from top (5) and lower part (6) of tree III; *s*, wide bands of sclerenchyma; figs. 7, 8, sections of suppressed year old shoots from top (7) and lower regions (8) of tree II; ×5.5.

SHOOTS FIVE TO NINETEEN YEARS OLD.—In general the three types of medullary rays previously described as characteristic of the white oak wood occur in all shoots from 5 to 20 years old, but there are three distinct types of compound rays: (1) rays which are broad, high, gradually tapering wedges, usually formed by the gradual widening of a single uniseriate or triseriate ray which has its origin at the pith; (2) compound rays, which are wide sheets of ray parenchyma formed by the aggregation of many small linear rays; (3) in addition to these broad rays there are "secondary" broad rays, formed as the stem increases in circumference, which originate abruptly some distance from the center, not by a gradual widening of a single ray nor as the result of the fusion of many small



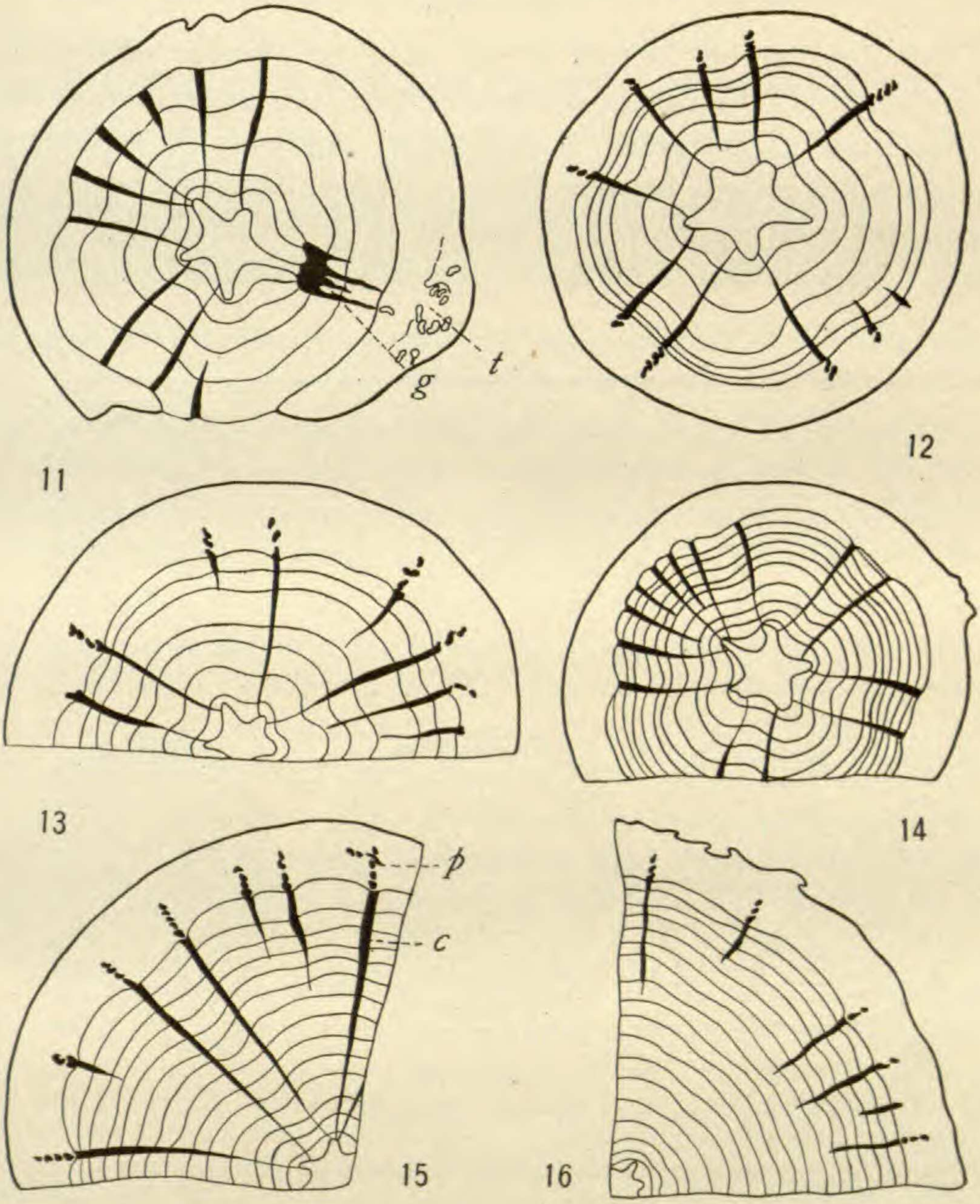
FIGS. 9, 10.—Transverse sections of portions of compound rays showing abrupt mode of origin of compound rays: uniseriate (*u*), multiseriate (*m*), and compound (*c*) rays; *f*, wood fibers; *t*, tracheids; *p*, thin-walled parenchyma marking boundary between rings of growth; ×200.

rays, but by a sudden checking of the development of all tracheidal tissue within the immediate vicinity of the ray and the consequent continued growth of parenchyma in this region. This abrupt change usually occurs at the beginning of a year's growth. Figs. 9 and 10 show transverse sections of portions of such rays at the points where they abruptly broaden, and illustrate very clearly the manner in which this type of ray originates. These three types of compound rays occur generally in all sections of the mature wood, but the wedge-shaped, gradually tapering ray, as seen in transverse section, appears to be the characteristic type of broad ray in this species of oak.

A very peculiar and constant feature of the multiseriate and compound rays is the manner in which they are broken up, upon entering the cortical region of the stem, into wedge-shaped masses of ray parenchyma. No such interruption or breaking up of the thin, linear uniseriate rays is apparent.

A careful study of different sections from the lower, central, and top regions of the same tree (figs. 11, 12, 13) makes it evident that the region of the tree from which the wood comes is only a slight factor, if any, in the modification of the ray system. On the other hand, a comparison of all sections of shoots of the same age from the three trees reveals a marked diminution in the diameters of stems from trees II and III, but this may be due chiefly to the effects of retardation in growth of these two trees rather than to a difference in age.

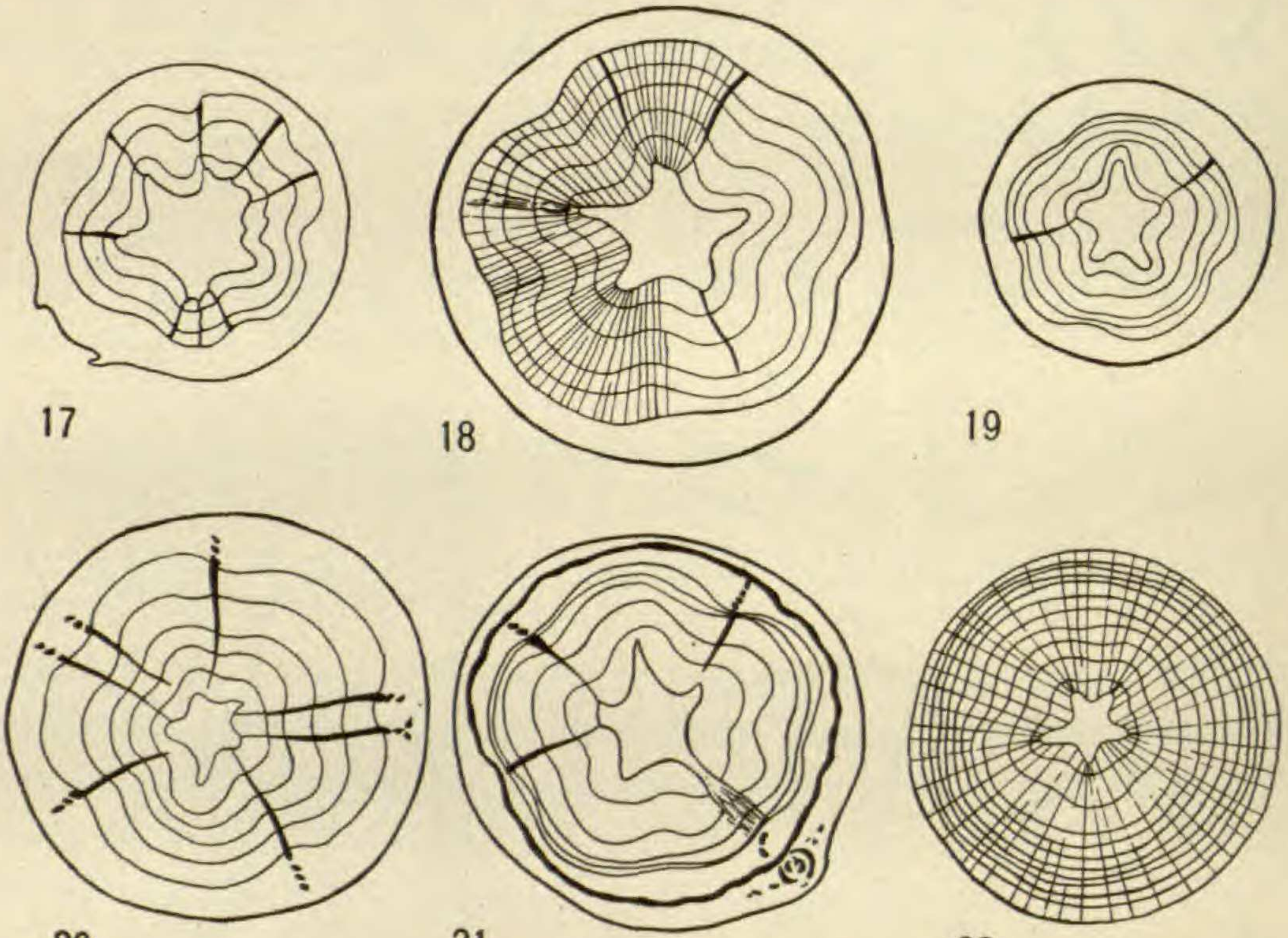
EFFECT OF SUPPRESSED GROWTH ON RAY SYSTEM.—The retarding effect of suppressed growth on the medullary ray development is easily seen in figs. 17, 18, and 19. Although wide rays occur in these suppressed twigs, they are neither so wide nor so deep as in the case of the vigorous shoots. Especially in some of the older stems from tree III the development of wide rays has been retarded to such an extent that only uniseriate rays occur, even in mature 11 and 12 year old wood (fig. 22); and in numerous specimens of wood 15–19 years old, taken from different regions of this same tree, wide rays are entirely absent up to about the tenth or eleventh year, when broad rays often appear abruptly, the phase of compounding being confined to one or two annual rings (fig. 16).



FIGS. 11–16.—Transverse sections: fig. 11, nodal section of 5 year old twig from lower part of tree I, showing well developed broad rays; *g*, leaf gap; *t*, leaf trace; figs. 12, 13, internodal sections of shoots from central (12) and top (13) regions of tree I; *c*, compound rays; fig. 14, section of 10 year old wood from tree III; fig. 15, section of vigorous 14 year old branch from central region of tree I; broad rays broken upon entering cortical region into wedge-shaped masses of ray parenchyma (*p*); fig. 16, section of suppressed 19 year old branch from tree III; figs. 11–14, ×5.5; figs. 15, 16, ×4⅛.

Discussion

Another notable feature of the wood of *Quercus alba* is its conspicuously ridged and depressed outline. Cross-sections of the twigs show 5 protruding wedge-shaped segments of secondary xylem which include between them 5 narrow, depressed segments, separated from the protruding ones by the great lateral leaf trace rays. This peculiar formation is especially noticeable in the stems of shoots 1–10 years old and gradually becomes less prominent in the older woods. BAILEY (2) accounts for this peculiarity of the oak wood on the ground that the medullary rays or storage tissue associated with the lateral leaf traces have a strong retarding influence on the surrounding tissue, thus accounting for the marked difference between the general rate of growth of the woody tissue


17 18 19 20 21 22

FIGS. 17–22.—Figs. 17–19, transverse internodal sections of 3 and 5 year old twigs from lower branches of tree III, showing retarded development of multiseriate rays; fig. 20, internodal section of 5 year old twig from top branch of tree II; fig. 21, section, cut near node, of 5 year old stem from upper branch tree III; fig. 22, section of suppressed 12 year shoot from central region of tree III; striking illustration of effect of suppressed growth upon medullary ray development; ×5.5.

and that of the large aggregate rays. When the rays are strongly developed, the dipping in of the annual ring where it crosses a large ray is sharper, thus explaining the narrow, depressed segments.

From observations of transverse sections of twigs from *Quercus alba*, *Q. bicolor*, and *Q. macrocarpa* I find that there is evidence of retardation in growth of the tissues in the immediate vicinity of the wide rays, especially noticeable in the marked dipping in of the annual rings where they cross the large rays. However, aside from a few extreme cases, this checking influence of the wide foliar rays does not explain the 5 conspicuous depressions so characteristic of the wood of *Quercus*. Their cause may be traced more directly to the effect of the leaf traces upon the general growth and form of the woody cylinder. Since the principal function of the xylem is the conduction of water from the soil to the outer parts of the plant, it is obvious that the maximum upward movement of solutions in the stem would be through the tracheidal tissues and vessels in direct line with the leaf traces. This would cause an acceleration in growth and the consequent outward projection of those 5 regions of the woody cylinder associated with leaf traces, while the neighboring conducting tissues, namely, the so-called depressions from which the main conducting streams had been diverted to the petioles of the leaves, would fail to maintain their normal rate of growth.

This condition of the secondary xylem may persist for a number of years, but there is a gradual diminution in the size of the depressions until at length the cambium layer and the xylem assume a circular outline. This may be due to the fact that as the wood increases in age its capacity for water conduction decreases, owing to the choking of the lumina of the vessels of the central regions of the wood with tyloses. In typical heart wood trees, such as the oak, the sap wood is limited in certain species to the youngest annual ring, and in some cases merely to the tracheary tissues of this ring. The narrowing of the active conducting zone would then be likely to cause a more even development of the woody tissues around the entire stem. A fact worthy of note in connection with this characteristic formation of the cambium and xylem in the stem of the oak is that corresponding to the degree of depression of the secondary xylem in the concave segments is the proportionate increase in amount of phloem above these segments.

With two exceptions, all of the seedlings used in this investigation were germinated and grown under greenhouse conditions, averaging 1.75–3 inches in height. Here, as in the case of the first annual ring, uniseriate rays are the prevailing type, multiseriate rays 3 and 4 cells in width appearing only in the vicinity of lateral leaf traces.

Summary

1. It was chiefly with the purpose of determining the effect of certain conditions upon the ray system of *Quercus alba*, such as the age of the trees, location of shoots in the trees, and vigorous or suppressed conditions of growth, that this investigation was undertaken.

2. The results obtained indicate that neither the age of the trees nor the location of wood in a tree is an appreciable factor in the modification of the ray system.

3. The conditions of vigorous and suppressed growth, however, are problems to be considered. With decreasing vigor of growth in the mature wood multiseriate rays appear at progressively later stages in the development of the stem.

4. Multiseriate rays, 2–6 cells in width, occur in the seedlings and the first annual ring of *Quercus alba* only in the vicinity of lateral leaf traces.

5. The peculiar formation of the cambium and wood in the stem of the oak, whereby 5 wedge-shaped segments of secondary xylem are formed, including between them 5 narrow depressed segments, is due directly to the influence of the outgoing leaf traces upon the general growth and form of the woody cylinder.

This investigation was undertaken at the Botanical Laboratory of Oberlin College, and the sincerest thanks of the writer are due to Professor FREDERICK O. GROVER and to Dr. SUSAN P. NICHOLS for their kind assistance. Grateful acknowledgment is also made of the valuable criticism and advice given by Dr. CHARLES J. CHAMBERLAIN and Dr. W. J. G. LAND during the continuation of the work at the University of Chicago.

UNIVERSITY OF CHICAGO

LITERATURE CITED

1. BAILEY, I. W., Reversionary characters of traumatic oak wood. BOT. GAZ. **50**:374–380. 1910.
2. ———, The relation of the leaf trace to the formation of compound rays in the lower dicotyledons. Ann. Botany **25**:225–241. 1911.
3. ———, The evolutionary history of the foliar ray in the wood of the dicots, and its phylogenetic significance. Ann. Botany **26**:647–661. 1912.
4. BAILEY, I. W., and SINNOTT, E. W., Phylogeny of the angiosperms. BOT. GAZ. **58**:36–58. 1914.
5. EAMES, A. J., On the origin of the broad ray in *Quercus*. BOT. GAZ. **49**:161–166. 1910.
6. ———, On the origin of the herbaceous habit in angiosperms. Ann. Botany **25**:215–224. 1911.
7. JEFFREY, E. C., The progress of plant anatomy during the last decade. Amer. Nat. **43**:230–237. 1909.
8. THOMPSON, W. P., On the origin of the multiseriate ray of the dicotyledons. Ann. Botany **25**:1005–1014. 1911.